



Effects of snow depth manipulation on the releases of carbon, nitrogen and phosphorus from the foliar litter of two temperate tree species

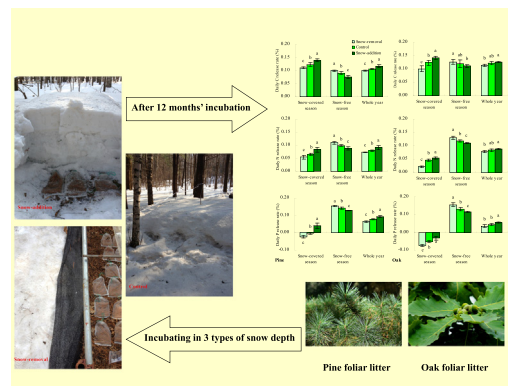
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HIGHLIGHTS

- Snow depth affected significantly the releases of C, N and P from foliar litter
- The release patterns were reverse between the snow-covered and snow-free seasons
- Snowpack promoted foliar litter C, N and P releases
- The releases of C, N and P from foliar litter were slowed by decreased snow depth associated with global climate change

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 3 February 2018
Received in revised form 25 June 2018
Accepted 25 June 2018
Available online 4 July 2018

Editor: Elena PAOLETTI

Keywords:

Snow depth manipulation
Temperate forest
Litter decomposition
Elemental release
Global climate change

ABSTRACT

The effect of snow depth on litter decomposition in cold regions has attracted substantial attention, but the importance of snow depth to the releases of carbon (C), nitrogen (N), and phosphorus (P) and the underlying mechanisms remain unclear. The releases of C, N, and P from the foliar litter of *Pinus koraiensis* and *Quercus mongolica* in response to snow depth changes were examined for 12 months in a temperate forest of Northeast China via a snow depth manipulation experiment that included snow-addition (SA), snow-removal (SR), and control (CK) treatments. We found that the SA treatment promoted the releases of C, N, and P from the foliar litter during the snow-covered season but slowed these processes during the following snow-free season; however, the SR treatment produced the opposite results. Compared with the CK treatment, the SA treatment increased the annual releases of C, N, and P by 2.52%, 0.50%, and 4.68%, respectively, whereas the SR treatment decreased the corresponding values. The elemental release during the snow-covered season was associated with the freeze-thaw cycle (FTC) and microbial biomass, whereas that during the snow-free season was mainly controlled by the temperature of the litter layer. Our findings indicated that the snow depth promoted the releases of C, N and P from the foliar litter of the two tree species, especially during the snow-covered season. These results deepen the understanding of the biogeochemical cycling in cold regions under global climate change scenarios.

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1. Introduction

The releases of carbon (C) and nutrients from litter play a critical role in the flow of energy and cycling of nutrients in forest ecosystems (Cornelissen and Cornwell, 2014; Berger et al., 2015). Litter provides

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Table 1

Basic characteristic of the three treatments at different sampling stages for the snow depth manipulation experiment.

Sampling stage	Decomposition days	Sampling date	SD (cm)			AT (°C)			PAT (°C)			NAT (°C)			FTC		
			SR	CK	SA	SR	CK	SA	SR	CK	SA	SR	CK	SA	SR	CK	SA
OF	49	2014/12/2	0c	4.1b	6.6a	−3.2a	−2.9a	−2.9a	20.2b	21.0b	25.9a	161.3a	138.0b	136.4b	31a	26b	24b
DF	145	2015/3/18	0c	21.5b	39.2a	−12.1b	−5.0b	−4.8a	0b	2.1ab	3.2a	1273.7a	519.9b	497.0b	8a	4b	0c
TS	176	2015/4/18	0c	6.2b	10.9a	1.6a	1.3a	0.6b	34.6c	61.9b	70.9a	17.1a	15.8a	8.7b	23a	21b	14c
ESF	239	2015/6/20	0a	0a	0a	12.2a	12.0a	12.6a	791.4a	774.0ab	740.8b	0a	0a	0a	14a	15a	16a
MSF	300	2015/8/20	0a	0a	0a	18.8a	18.7a	18.8a	1128.0a	1124.3a	1126.8a	0a	0a	0a	0a	0a	0a
LSF	366	2015/10/25	0a	0a	0a	11.3a	11.5a	11.3a	756.9a	771.5a	759.5a	0a	0a	0a	10a	7a	9a

OF, onset of freezing stage; DF, deep freezing stage; TS, thawing stage; ESF, early snow-free stage; MSF, middle snow-free stage; LSF, late snow-free stage; CK, the control treatment; SA, the snow-addition treatment; SR, the snow-removal treatment; SD, snow depth; AT, litter layer daily average temperature; PAT, litter layer positive accumulated temperature; NAT, litter layer negative accumulated temperature; FTC, frequency of the freeze-thaw cycle in litter layer.

The values for SD ($n = 15$), AT ($n = 3$), PAT ($n = 3$), NAT ($n = 3$) and FTC ($n = 3$) are the means; the different lowercase letters in the table indicate a significant difference in different treatments within the same variable ($p < 0.05$, Bonferroni correction).

an integrative framework that links plants and ecosystems from the perspective of elemental stoichiometry (Sternner and Elser, 2002). Climate, soil moisture and microorganisms predominantly regulate the releases of C and nutrients from litter (Pastor and Post, 1986; Hobbie and Chapin III, 1996), and the releases may be changed by snowpack significantly, especially in cold regions (Fitzhugh et al., 2001; Schimel et al., 2004; Groffman et al., 2011). Although the ecological importance of the interactions among snowpack, temperature, soil moisture, and microbial activity have been widely investigated (Mackelprang et al., 2011; Robroek et al., 2013), the effects of snow depth changes on the releases of C and nutrients from litter have seldom been evaluated. Such studies are important for modeling and predicting the effects of global climate change on the biogeochemical cycling in terrestrial ecosystems (Aerts, 2006).

Many studies have reported that the warmer temperature under thick snowpack increases the rates of litter decomposition and elemental release (e.g. Nadelhoffer et al., 1991; Jonasson et al., 1999; Wu et al., 2014b), however, Aerts et al. (2012) argued that snow addition had limited effects on litter N dynamics. This discrepancy implies that the directions, magnitudes and drivers of the effects of snowpack on elemental release during litter decomposition may vary with other factors such as snow depth and season (O'leary and Seastedt, 1994; Baptist et al., 2010). In addition, it is still unclear how snow depth responds to global climate change. Generally, the snow depth decreased during the 20th century (Mote et al., 2005), but feedback between regional or local climate and global climate change resulted in increases in the snow depth in some regions (Beniston et al., 2003). Therefore, exploring how snow depth changes affect the releases of C, nitrogen (N) and phosphorus (P) during litter decomposition is crucial to understand the responses of forest ecosystem processes to global climate change.

Snowpack is an effective insulator, that protects soils from low air temperature in winter and keeps the microenvironment warm and moist (Mackelprang et al., 2011) and the decomposers active (Bokhorst et al., 2013); thus, snowpack accelerates litter decomposition (Saccone et al., 2013) and elemental release (Freppaz et al., 2008). Additionally, snowmelt favors the releases of C and nutrients from litter (Hobbie and Chapin III, 1996; Liu et al., 2016). Nevertheless, at sites with little or no snowpack, frequent freeze-thaw cycles (FTCs) in early spring may damage the physical structure and increase the decomposability of litter, and consequently, increase the rate of C and nutrient releases from the litter in the following snow-free season (Wu et al., 2010). Clearly, snow depth changes create diverse microenvironments and decomposer activities and consequently result in uncertain impacts on elemental release during litter decomposition, and these impacts need to be comprehensively assessed.

The temperate forests in northeastern China account for one-third of the forest resources in China (both stocking volume and area) and play a critical role in the global C budget and nutrient cycle (Wang, 2006). This forest ecosystem is characterized by seasonal snowpack in winter (from November to April of the following year) that is sensitive to ongoing climate change (Wang et al., 2013). To explore the effects of snow depth changes on elemental release from the foliar litter, we performed a snow depth manipulation experiment that included three treatments (i.e., control, CK; snow-removal, SR and snow-addition, SA) and used the litterbag method to investigate the releases of C, N and P from the foliar litter of Korean pine (*Pinus koraiensis*) and Mongolian oak (*Quercus mongolica*) from October 2014 to October 2015. Our specific objectives were to (1) quantify the dynamics of C, N and P releases from the foliar litter of the two contrasting tree species under the three treatments in both snow-covered and snow-free seasons; and

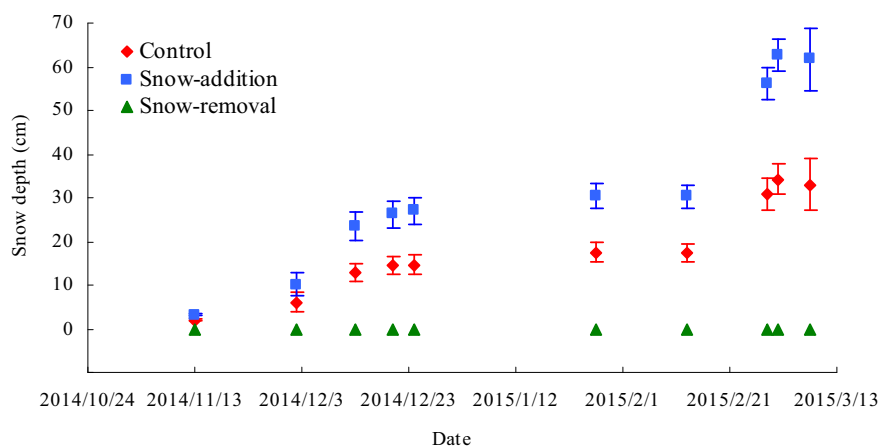


Fig. 1. Snow depth after each snowfall across snow depth manipulation treatments (mean \pm SD, $n = 15$). The differences among the treatments are significant during the entire experimental period ($p < 0.05$, Bonferroni correction).

Table 2Regression equation between daily elemental release rate (Y) and related factors (F).

		Equation	R^2	p	SSR	F	df
Snow-covered season	Daily C release rate	$Y = -0.024 - 0.056 F_1 + 0.053 F_2 + 0.130 F_3$	0.836	<0.001	0.102	38.540	53
	Daily N release rate	$Y = 0.063 + 0.053 F_2 + 0.075 F_3$	0.766	<0.001	0.202	36.159	53
	Daily P release rate	$Y = 0.114 + 0.049 F_2 + 0.083 F_3$	0.568	<0.001	0.300	24.770	53
Snow-free season	Daily C release rate	$Y = 0.095 + 0.024 F_1 + 0.020 F_2$	0.649	<0.001	0.085	18.542	53
	Daily N release rate	$Y = -0.033 + 0.073 F_1$	0.666	<0.001	0.306	41.394	53
	Daily P release rate	$Y = -0.098 + 0.059 F_1$	0.511	<0.001	0.459	18.333	53

 F_1 , Factor 1, "Temperature"; F_2 , Factor 2, "Microbial biomass"; F_3 , Factor 3, "FTC".

(2) explore the factors controlling the C, N and P releases. We hypothesized that (1) the increased snow depth would promote the elemental release from the foliar litter during the snow-covered season because of the insulation from the snowpack, whereas it would slow this process during the following snow-free season because of the fewer remaining labile components and the shorter snow-free season; and (2) in contrast, the decreased snow depth would slow the elemental release from the foliar litter during the snow-covered season due to a lack of insulation from the snowpack, but it would promote this process during the snow-free season because of more remaining decomposable components.

2. Materials and methods

2.1. Site description

The site is located at the Maershan Forest Ecosystem Research Station, Northeast China (127°30'E, 45°20'N, 400 m a.s.l.). The climate is a continental monsoon climate with a windy and dry spring, a warm and humid summer, and a dry and cold winter. The mean annual precipitation and air temperature are 629 mm and 3.1 °C, respectively. The soil is classified as Haplumbrepts. The snowpack lasts for ~150 days (from November to the following April) with a mean snow depth of 24 cm.

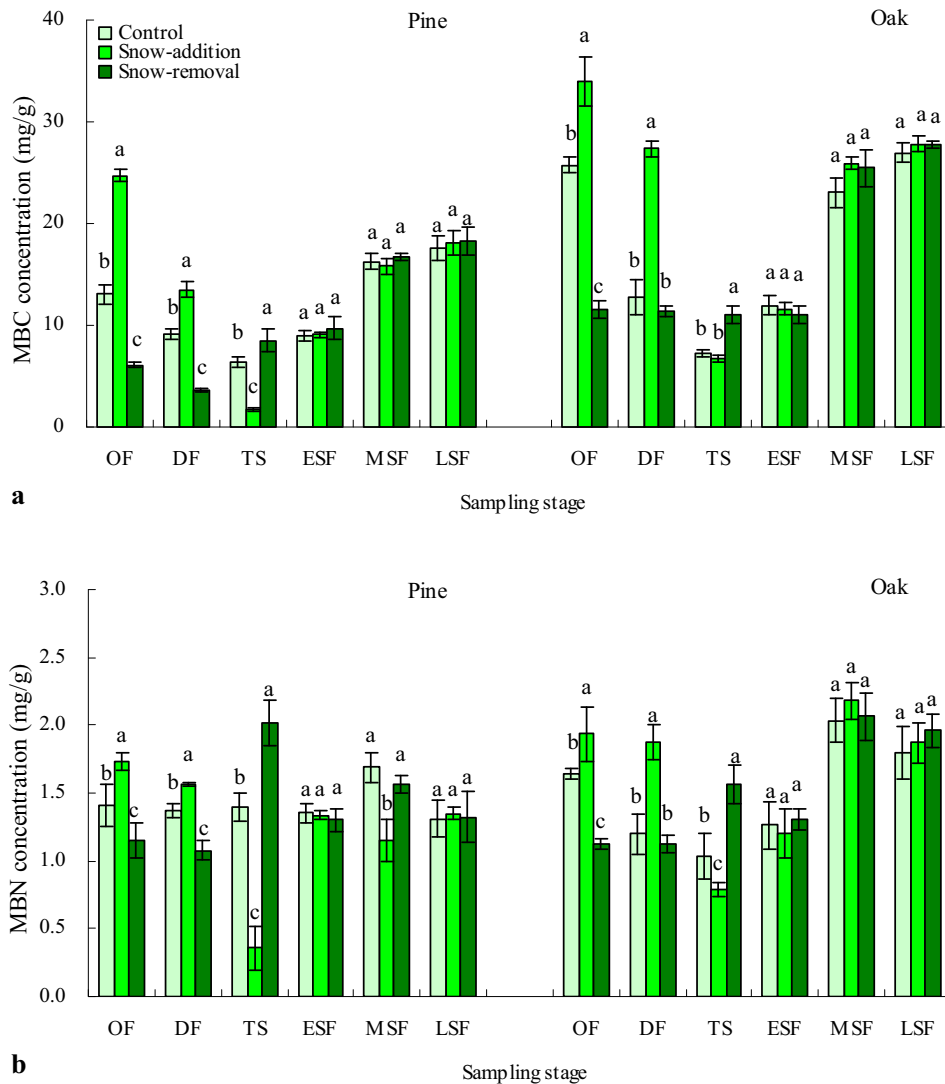


Fig. 2. Foliar litter microbial biomass carbon (MBC, a) and nitrogen (MBN, b) concentrations of both species across snow depth manipulation treatments (mean \pm SD, $n = 3$). The different lowercase letters indicate a significant difference within the same variable ($p < 0.05$, Bonferroni correction); OF, onset of freezing stage; DF, deep freezing stage; TS, thawing stage; ESF, early snow-free stage; MSF, middle snow-free stage; LSF, late snow-free stage.

(Wang et al., 2013). The current forests are temperate deciduous forest stands and plantations (Wang et al., 2013).

2.2. Snow depth manipulation

Snow depth manipulations were carried out from November 2014 to April 2015 with a split-plot blocking design. Three 30 m

× 20 m fixed plots were randomly established in a Korean pine plantation (planted in 1965) in September 2014. The mean stand density, diameter at breast height, and height were 3145 trees ha⁻¹, 12.9 cm, and 12.1 m, respectively. Within each fixed plot, three 5 m × 5 m sub-plots, representing three treatments (CK, SA and SR) were established with 3–4 m intervals in between to minimize potential disturbances induced by the treatments. The SR treatment was

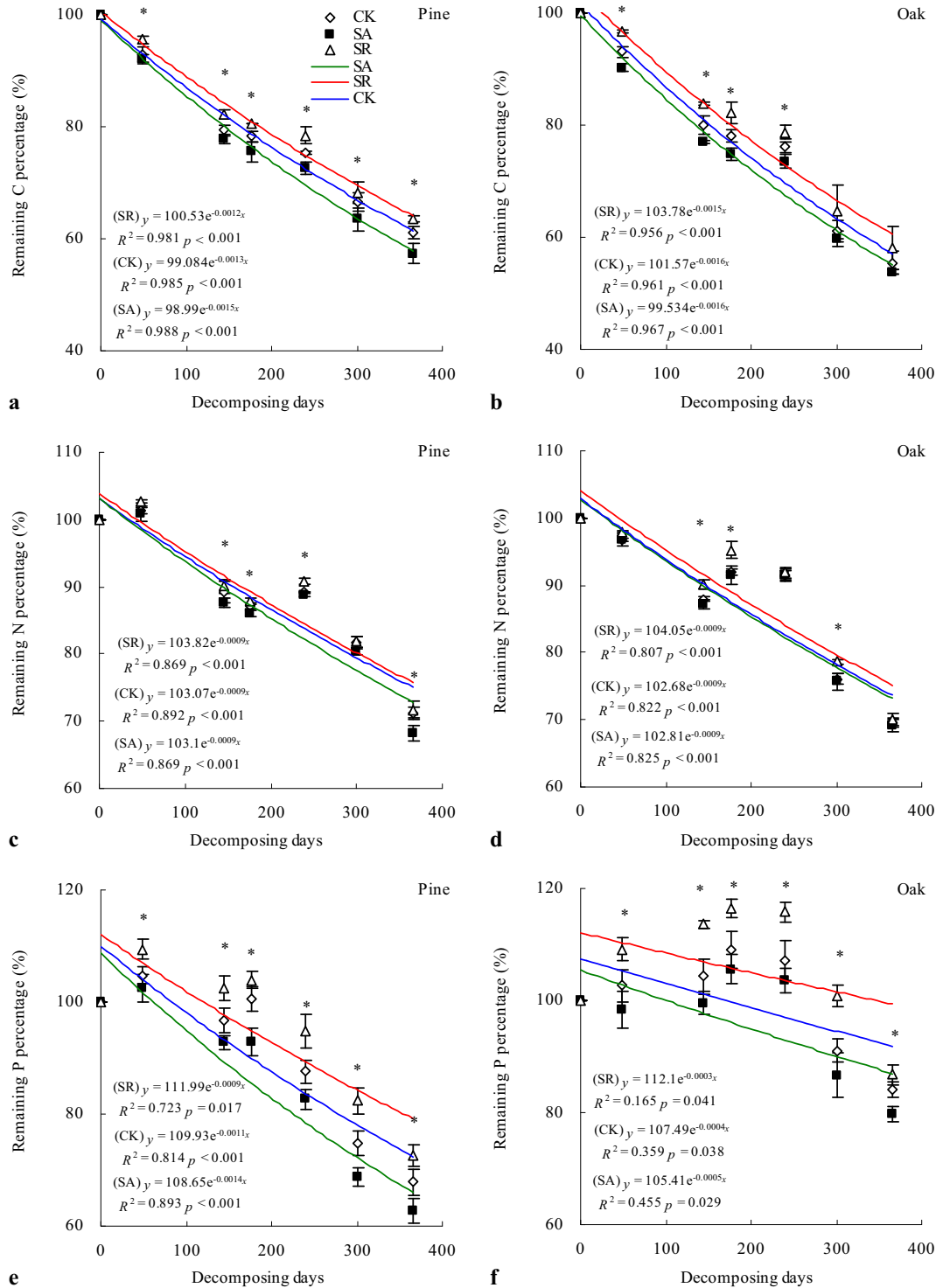


Fig. 3. Remaining percentages (P_m) of the C (a, b), N (c, d) and P (e, f) in different decomposing days (sampling stages) across snow depth manipulation treatments (mean, $n = 3$). *Significant difference at $p < 0.05$ (Bonferroni correction); CK, the control treatment; SA, the snow-addition treatment; SR, the snow-removal treatment. Results of two-way ANOVA suggested significant effects of snow depth ($F = 14.64$ to 101.31 , $p < 0.001$, Supplementary Table S2), sampling stage ($F = 50.03$ to 779.44 , $p < 0.001$, Supplementary Table S2) and the interaction of snow depth and sampling season ($F = 4.56$ to 9.51 , $p < 0.05$, Supplementary Table S3) on the remaining percentages of the C, N and P.

implemented with a custom-designed frame that was made of a marine grade light alloy (2.5 m × 2.5 m × 0.3 m) covered with transparent plexiglass (Shanghai Shen'er Plastic Co., Ltd., euphotic index >92%). Each side of the frame was surrounded by a screen to prevent the entry of snow but ensure adequate ventilation inside. Immediately after each snowfall, the snow on the frame was collected and transferred to the SA treatment using a large-pore screen to mimic in situ snowfall. The CK treatment was left undisturbed. A 20 cm deep trench was dug around each subplot to prevent the effect of

snowmelt in early spring. The frames in all SR treatments were removed during the snow-free season (from May to October).

2.3. Litter decomposition experiment

The litterbag method was used to quantify the releases of C, N and P from the foliar litter. In September 2014, fresh pine and oak foliar litter were collected from the forest floor and air-dried for 2–4 weeks. Five samples for each species were taken and oven-dried at 70 °C for 48 h

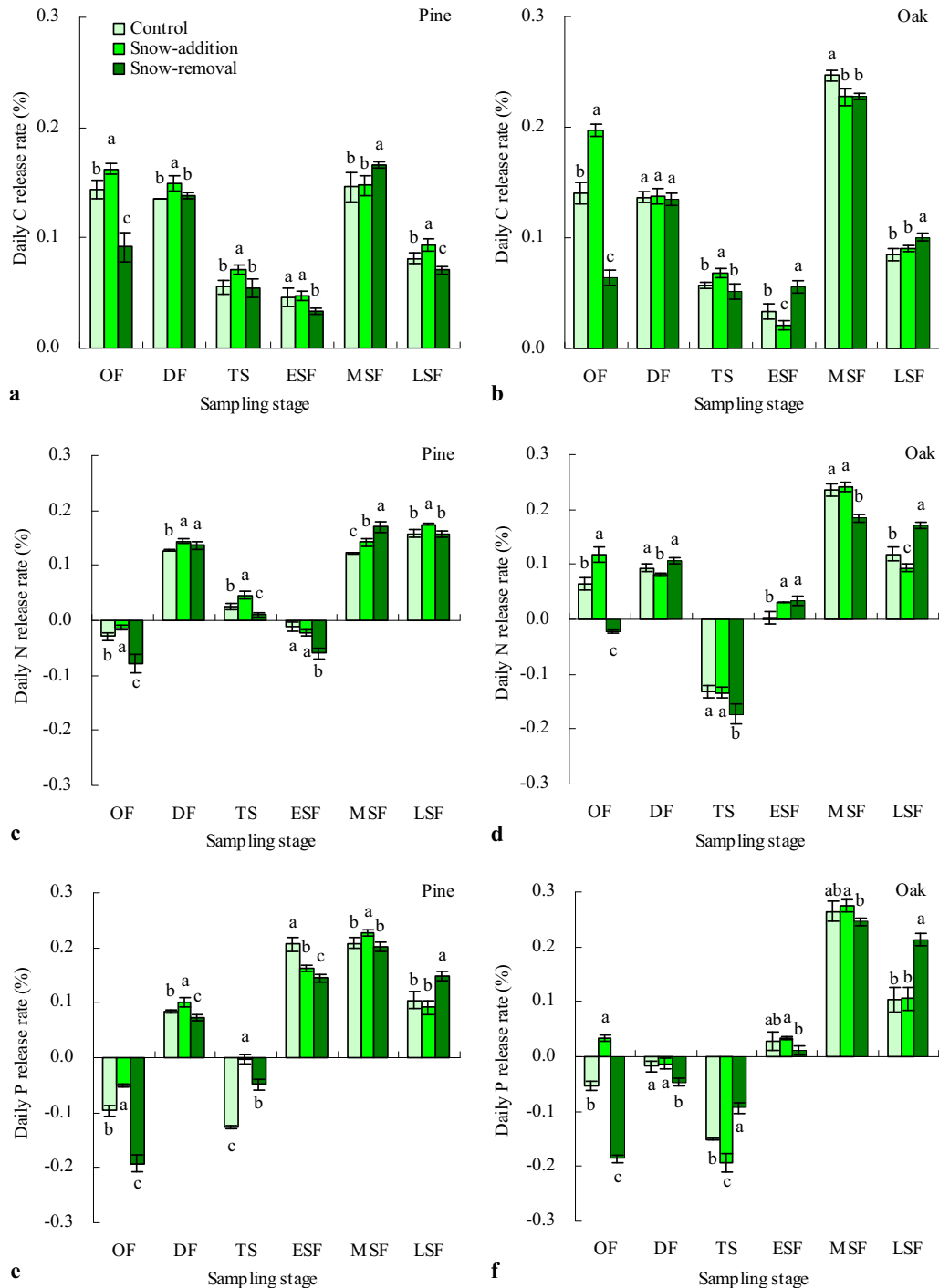


Fig. 4. Daily release rates (L_d) of the C (a, b), N (c, d) and P (e, f) in different decomposing days (sampling stages) across snow depth manipulation treatments (mean \pm SD, $n = 3$). CK, the control treatment; SA, the snow-addition treatment; SR, the snow-removal treatment; OF, onset of freezing stage; DF, deep freezing stage; TS, thawing stage; ESF, early snow-free stage; MSF, middle snow-free stage; LSF, late snow-free stage. Results of two-way ANOVA suggested significant effects of snow depth ($F = 1.85$ to 5.86 , $p < 0.05$, Supplementary Table S4), sampling stage ($F = 19.55$ to 156.56 , $p < 0.001$, Supplementary Table S4) and the interaction of snow depth and sampling season ($F = 3.43$ to 26.85 , $p < 0.05$, Supplementary Table S5) on the daily release rates of the C, N and P.

to determine the dry mass and initial chemical compositions (Supplementary Table S1). Meanwhile, the air-dried foliar litter samples were placed inside nylon litterbags (15 × 20 cm with 1 mm mesh size, 10 g of litter per litterbag), and the edges of the bag were sealed. Then, the litterbags were placed on the forest floor after the litter layer was removed on October 25, 2014, and the litterbags were placed at intervals of at least 2 cm in between to avoid potential disturbance.

According to Olsson's protocol (Olsson et al., 2003), we divided the experimental year into six stages, i.e., onset of freezing stage (December 2014), deep freezing stage (March 2015), thawing stage (April 2015), early snow-free season (June 2015), middle snow-free season (August 2015) and late snow-free season (October 2015) (Table 1). At the end of each stage, three litterbags per tree species were collected from each treatment. A total of 324 litterbags (3 plots × 3 treatments × 2 species × 6 sampling stages × 3 bags) were sampled in this study.

Meanwhile, the iButton DS1923-F5 Recorders (Maxim Integrated Products, Inc., Sunnyvale, TX, USA) were used to record the temperature at the litter layer in each treatment and the air atmosphere every 1 h from October 25, 2014 to October 25, 2015. The snow depth was obtained by averaging the direct measurements at 15 random locations for each treatment that were collected with a ruler after each snowfall event (Fig. 1, Table 1).

2.4. Laboratory analysis

When the litterbags were harvested, we first removed the foreign objects (e.g., arthropods, roots) from the litter and then divided the litter into two parts. One part (~20% of the sample) was stored in a cool area at 4 °C to determine the microbial biomass carbon (MBC) and nitrogen (MBN) concentrations; the other part was oven-dried at 70 °C for 48 h to determine the dry mass and concentrations of C, N and P.

The MBC and MBN concentrations were determined from the differences between unfumigated and fumigated samples using the dichromate oxidation-ferrous sulfate titration method and indigotic colorimetry method for the extraction with 0.5 mol/L K₂SO₄ (Edwards et al., 2006). The C and N concentrations were determined with a Multi N/C 3000 analyzer with 1500 Solids Module (Analytik Jena AG, Germany). The P concentration was determined using the phospho-

molybdenum yellow spectrophotometry method (TU-1901, Puxi Ltd., Beijing, China). The lignin and cellulose contents were determined with the acid detergent lignin method (Vanderbilt et al., 2008). All chemical analyses were performed in triplicate and finished within 2 weeks after the field sampling.

2.5. Data analysis

For each sampling stage, the daily average temperature (AT), positive accumulated temperature (PAT) and negative accumulated temperature (NAT) at the litter layer, and the frequency of freeze-thaw cycle (FTC) were calculated (Table 1). One FTC was defined as a cycle when the temperature decreased below 0 °C or increased above 0 °C for at least 3 h followed by an increase above 0 °C or decrease below 0 °C for at least 3 h (Zhu et al., 2012). The remaining contents (R_m), remaining percentages (P_m) and daily release rates (L_t) of the C, N and P were calculated as follows:

$$R_m = M_t \times C_t \quad (1)$$

$$P_m = R_m / R_{mt0} \quad (2)$$

$$L_t(\%) = [(R_{m(t-1)} - R_{mt}) / R_{mt0}] / D_{\Delta t} \times 100\% \quad (3)$$

where M_t is the dry mass of the litter at stage t ; C_t is the concentration of C, N, or P at stage t ; R_{mt0} is the initial dry mass of the litter; $R_{m(t-1)} - R_{mt}$ is the remaining C, N, or P content between stages $t-1$ and t ; R_{mt0} is the initial C, N, or P content; $D_{\Delta t}$ is the number of days between stages $t-1$ and t .

MBC and MBN were calculated as follows:

$$MBC = EC / k_{EC} \quad (4)$$

$$MBN = EC / k_{EN} \quad (5)$$

where EC and EN are the differences between organic C and N extracted from fumigated and nonfumigated foliar litter, respectively; k_{EC} equals 0.38 (Vance et al., 1987) and k_{EN} equals 0.45 (Brookes et al., 1985).

An independent t -test with $\alpha = 0.05$ was used to evaluate the differences in the initial chemical compositions of the foliar litter between the two species. A one-way ANOVA (with Bonferroni correction) was used to assess the differences in the environmental variables, remaining percentages and daily release rates at the same stages among the treatments. After the pair-wise comparisons tests were conducted with a MANOVA procedure, the responses of the remaining percentage for the treatments to the sampling stage (decomposing days) were evaluated with a nonlinear regression. Log-transformation was used, if necessary, to meet the requirement of variance homogeneity. A generalized linear model (GLM) procedure was performed to evaluate the main effects of snow depth and sampling stage or snow depth and sampling season on the remaining percentage and daily release rate. A factor analysis was used to describe the linking among AT, PAT, NAT, FTC and MBN. After achieving new factors, multiple linear regression was conducted to evaluate the responses of the daily release rate to the new factors. All statistical analyses were performed using SPSS 20.0 for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Carbon release

The statistical results showed that snow depth, sampling stage and the interaction of snow depth and sampling season had significant effects on the remaining C percentage ($p < 0.05$) (Supplementary Table S2, S3). The remaining C percentage showed a clear increasing tendency along the snow depth gradient from the SA treatment to the CK and SR treatments at each sampling stage (Fig. 3a, b). After one year, the remaining C percentages after decomposition from the SA to

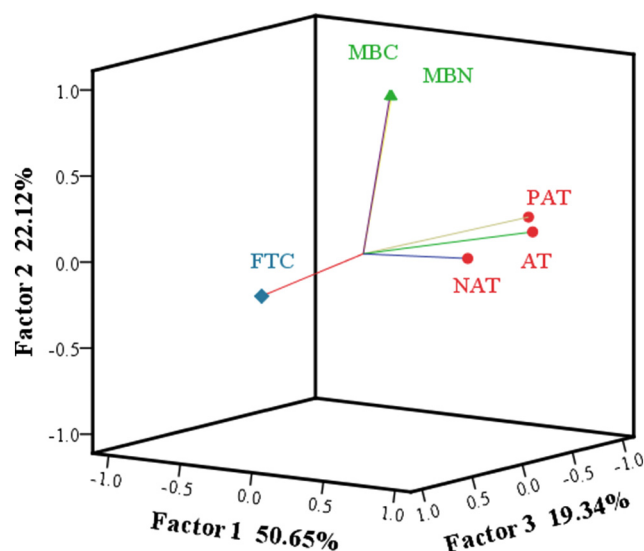


Fig. 5. Common factors evaluated from AT, PAT, NAT, FTC, MBC and MBN by factor analysis. AT, litter layer daily average temperature; PAT, litter layer positive accumulated temperature; NAT, litter layer negative accumulated temperature; FTC, frequency of the freeze-thaw cycle in litter layer; MBC, foliar litter microbial biomass carbon concentration; MBN, foliar litter microbial biomass nitrogen concentration. The loadings of AT, PAT, NAT, FTC, MBC and MBN was 0.893, 0.742, 0.922, 0.961, 0.915 and 0.912, respectively.

SR treatments ranged from 57.3–63.6% for the pine foliar litter and 53.7–58.1% for the oak foliar litter. A large amount of C release occurred during the snow-covered season, when 53.4–57.4% and 42.6–54.4% of C release occurred for pine and oak, respectively. The snow-covered season was as critical as the snow-free season for C release. In the SA treatment, the amount of remaining C after one year was 5.13% lower for pine and 2.52% for oak than that in the CK treatment and in the SR treatment, the remaining C was 4.43% and 2.71% higher than that in the CK treatment for pine and oak, respectively.

Snow depth, sampling stage and the interaction of snow depth and sampling season had significant effects on the daily C release rate ($p < 0.05$) (Supplementary Table S4, S5). The daily C release rate decreased from the onset of freezing stage to the early snow-free season and increased throughout the remaining time (Fig. 4a, b). There was a significant decreasing tendency in this rate with the reduction in snow depth during the snow-covered season ($p < 0.05$). Meanwhile, a significant opposite relationship appeared during the snow-free season ($p < 0.05$).

3.2. Nitrogen release

The statistical results showed that snow depth, sampling stage and the interaction of snow depth and sampling season significantly affected the remaining N percentage ($p < 0.05$) (Supplementary Table S2, S3). Fig. 3c, d indicates that the remaining N percentage was highest in the SR treatment, moderate in the CK treatment, and lowest in the SA treatment in the same sampling stages. The N release from pine was 28.3–31.8% in the SR and SA treatments, and that of oak was 30.0–30.8%. The remaining N percentage decreased by 3.01% for pine and 0.50% for oak after one year in the SA treatment compared with the CK treatment; meanwhile, the remaining N percentage increased by 0.46% and 0.44%, respectively, in the SR treatment. The pine foliar litter displayed N enrichment between the onset of freezing stage and the early snow-free season, while that of oak displayed N enrichment between the onset of freezing stage and the thawing stage (Fig. 3c, d).

Snow depth, sampling stage and the interaction of snow depth and sampling season significantly affected the daily N release rate ($p < 0.05$) (Supplementary Table S4, S5). The daily N release rate of pine increased from the onset of freezing stage to the deep freezing stage, then decreased until the early snow-free season, and increased again for the remaining time (Fig. 4c, d). The daily N release rate of oak decreased from the onset of freezing stage to the early snow-free season and increased again for the remaining time. Significant differences in the daily N release rates were found among the different treatments in the snow-covered and snow-free seasons ($p < 0.05$). During the snow-covered season, the highest rates were observed in the SA treatment, the lowest values were observed in the SR treatment. The opposite trends were observed during the snow-free season.

3.3. Phosphorus release

The statistical results showed that snow depth, sampling stage and the interaction of snow depth and sampling season significantly affected the remaining P percentage ($p < 0.05$) (Supplementary Table S2, S3). In all six sampling stages, the highest remaining P percentages were observed in the SR treatment, while the lowest values were observed in the SA treatment (Fig. 3e, f). Over the whole year of decomposition, 27.4–37.2% of the P was released from the pine, and 13.2–20.2% was released from the oak. Compared with the CK treatment, the remaining P percentage of the whole year decreased in the SA treatment by 5.14% for pine and 4.68% for oak, while this percentage increased by 4.43% and 2.59% for pine and oak, respectively, in the SR treatment. The pine displayed P enrichment between the onset of freezing stage and the thawing stage, while the oak displayed P enrichment throughout the snow-covered season (Fig. 3e, f).

Snow depth, sampling stage and the interaction of snow depth and sampling season significantly affected the daily P release rate ($p < 0.05$) (Supplementary Table S4, S5). Except for the oak in the SA treatment, the daily P release rates increased from the onset of freezing stage to the middle snow-free season and decreased during the remaining time (Fig. 4e, f). There were also significant decreasing tendencies in the daily P release rates with the reduction in the snow depth during the snow-covered season ($p < 0.05$). Significant opposite relationships were observed during the snow-free season ($p < 0.05$).

3.4. Driving factors of elemental release

Three new factors were identified by the factor analysis: these factors explained 50.65%, 22.12% and 19.34% of the total diversity (Fig. 5). The loadings of NAT (0.922), AT (0.893) and PAT (0.742) were high in Factor 1 which was named “Temperature”. Factor 2 was named “Microbial biomass” because the loadings of MBC (0.915) and MBN (0.912) were high. In Factor 3, the loading of FTC (0.961) was high: this factor was named “FTC”. The releases of C, N and P from the foliar litter was associated with the FTC and microbial biomass during the snow-covered season ($R^2 > 0.568$, $p < 0.001$ in Table 2), while the temperature of the litter layer was the key factor that controlled the release of elements during the snow-free season ($R^2 > 0.511$, $p < 0.001$ in Table 2).

4. Discussion

4.1. C, N and P release during the snow-covered season

The results of this study were consistent with the hypotheses that the SA treatment would promote the releases of C, N, and P from the foliar litter during the snow-covered season, and the SR treatment would slow these releases. This study found that the daily release rates of C, N, and P during the snow-covered season decreased significantly in the order of SA > CK > SR. A previous study demonstrated that the thicker snowpack was an effective soil insulator (Jusselme et al., 2016), that kept the soil warmer than the areas with thin or absent snowpack (Mackelprang et al., 2011), and most of the decomposers were more active under thicker snowpack conditions (Robroek et al., 2013). A stable environment and active microbial activities were critical to the release of elements. In this study, we found that MBC and MBN increased along with the snow depth gradient from the SR treatment to the SA treatment from the onset of freezing stage to the deep freezing stage, and the releases of C, N, and P from the foliar litter was associated with MBC and MBN during the snow-covered season. Meanwhile, the daily release rates of C, N, and P were much lower in the SR treatment because of the colder microenvironment and lower microbial activity due to snow removal. Additionally, the multiple linear regression also showed that the FTC was the driving factor of the release of elements from the foliar litter during the snow-covered season (Table 2). These results are in accord with the results of the study by Wu et al. (2010).

4.2. C, N and P release during the snow-free season

Our hypotheses that the SR treatment would promote the releases of C, N, and P from the foliar litter during the snow-free season, and the SA treatment would slow those processes were supported by our data. The following underlying mechanisms could explain these different trends: First, compared with thin or absent snowpack, more labile components might be degraded during the snow-covered season under the thicker snowpack resulting from snow addition, which would reduce the foliar litter decomposition rate and the releases of C, N and P during the following snow-free season (Tomaselli, 1991). In addition, snow addition could lengthen the snow-covered season while shortening the snow-free season (Walker et al., 1999; Starr et al., 2000), the stable environment during the snow-free season was more favorable for decomposers

and accelerated the elemental release process (Berg and McLaugherty, 2003). The multiple linear regression sufficiently proved this theory, and the result showed that the environmental temperature was a dominant factor for elemental release during the snow-free season (Table 2). Finally, the more frequent FTC during the snow-covered season in the SR treatment damaged the physical structure of the foliar litter and increased the decomposability in the following snow-free season (Wu et al., 2010; Christenson et al., 2010), which also promoted the process of elemental release. The results of the multiple linear regression completely supported this finding (Table 2). As a result, the combination of the above factors produced an increase in the daily C, N, and P release rates in the SA treatment compared to the SR treatment during the snow-free season, which was consistent with our hypotheses.

4.3. The seasonal effects on the releases of C, N and P

We also observed that half of the foliar litter C was released during the snow-covered season, which is consistent with the findings of Wu et al. (2014a). This pattern occurred because most of labile C components, such as polymerized nutrients, acid-soluble extractive and cellulose, would decay during this period (Cotrufo et al., 2013). Additionally, the physical structure of the foliar litter could be directly damaged by the FTC or wet-dry cycle events during this period, which would directly increase the decomposability of the foliar litter (Taylor and Parkinson, 1988). During the snow-covered season, the thicker snowpack in the SA treatment supported high microbial activity, which contributed to foliar litter decomposition (Aerts, 1997). However, foliar litter in the SR treatment was often exposed to extreme subfreezing temperatures and more FTCs (Table 1), which reduced the microbial enzyme activity during the snow-covered season (Kuttim et al., 2017). Accordingly, there was a decreasing tendency in the C release from the foliar litter from the SA to SR treatments during the snow-covered season. Due to the lack of a snowmelt process during the snow-free season in the SR treatment, the microenvironment could more quickly restore to the appropriate temperature for microbial activity as the temperature increased (Hicks Pries et al., 2013), which explained why the higher daily rate of C release was observed in the SR treatment during the snow-free season (Fig. 4a, b).

In cold regions, temperatures are consistently below 0 °C and the soil undergoes deep freezing during the snow-covered season (Table 1); thus, the N and P release from the foliar litter might be more attributed to microbes than temperature in these areas (Tan et al., 2014). Before the decomposition of low-quality foliar litter (low N or P concentration), soil microorganisms have to absorb extra nutrients such as N and P from the soil to form proteins for their bodies (Hodges, 2010). Thus, soil microorganisms can begin to decompose foliar litter only when the nutrient levels meet their demands (Aponte et al., 2012). Findings by Moore et al. (2011) based on a decomposition experiment spanning 12 years in Canada indicated that net N release from litter occurred at a C:N ratio in the range of 33 to 68. In our study, the initial C:N ratios of pine and oak foliar litter were 107 and 71 (Supplementary Table S1), which were more than the critical value according to Moore et al. (2011); thus, the foliar litter N and P of both species displayed immediate enrichment during the onset of freezing stage (Fig. 3a–d). Our result suggested that microbes were the decisive factors for foliar litter N and P release during the snow-covered season, and the warmer and wetter conditions in the SA treatment should be beneficial for microbial activity during the snow-covered season (Hicks Pries et al., 2013). Additionally, during the thawing stage, the intense leaching effect of snowmelt also promoted the process of N and P release (Stanton et al., 1994). The results of this study illustrated that snow depth combined with the FTC and microbial biomass during the snow-covered season promoted the process of foliar litter N and P release in the temperate forest (Table 2).

Furthermore, the levels of foliar litter N and P in both species in all treatments also displayed enrichment during the snow-free season, indicating that the nutrient release process during the snow-free season was affected by the environmental temperature without the effect of snow depth (Vesterdal, 1999). Due to the snowmelt process, the environmental temperature increased sharply (Table 1), and the microbial activity recovered rapidly (Fig. 2); thus, more microbes participated in the decomposition process, and the nutrient contents increased (Zhou et al., 2011). On the other hand, after the intense leaching effect during the snow-covered season, the nutrient levels of foliar litter were not sufficient to support decomposition during the snow-free season, and the microbes had to absorb extra nutrients from the soil (Hobbie et al., 2012). Additionally, high temperatures together with high soil moisture contents could promote denitrification (Sharma et al., 2006; Kreyling et al., 2008). As a result, the combination of the above factors resulted in nutrient enrichment during the snow-free season (Fig. 3c–f). Moreover, the P mineralization dynamics were more related to environmental temperature than the N mineralization dynamics (Moore et al., 2011), and the P release rates from the foliar litter were higher at higher temperatures (Aerts et al., 2012). Accordingly, our findings indicated that the temperature during the snow-free season promoted the releases of N and P from the foliar litter (Table 2).

Although our experiment ran for 12 months to clarify the dynamics of foliar litter C, N and P release in the early stage of decomposition, a longer experimental design in which litter from more species and different forest ecosystems is still needed. Moreover, we must acknowledge that further studies with more frequent sampling rates than those in this study are also required to provide insights into the role of snow depth in C, N and P cycling.

5. Conclusions

The dynamics of C, N and P releases from the foliar litter displayed clearly increasing tendencies along the snow depth gradient from the SR to SA treatments during the snow-covered season, while the reverse patterns were observed during the snow-free season. In general, snow addition promoted elemental release, while snow removal slowed elemental release. In addition, the elemental release during the snow-covered season was associated with the FTC and microbial biomass; meanwhile, the temperature of the litter layer was the factor that influenced the elemental release during the snow-free season. These findings indicate that increased snow depth combined with the FTC and microbial biomass promotes the C and nutrient releases from the foliar litter; however, the process of elemental release may be limited by decreased snow depth associated with global climate change. In the future, further attention should be paid to the effects of snowpack in winter on ecological processes such as litter decomposition, nutrient cycling, and soil CO₂ efflux in forest ecosystems.

Acknowledgements

I am indebted to Dr. Elena Paoletti and the anonymous reviewers for their insightful comments and constructive suggestions that improved the manuscript. I also want to thank Xiankui Quan, Jia Dou and Juan Zhao for their help with the field sampling and laboratory analyses, as well as to Zhenfeng Xu, Wei He and Kai Yue for the nice suggestions on the early draft. The critical and constructive comments made by Dr. Chuankuan Wang are gratefully acknowledged. I also acknowledge China Scholarship Council for supporting a joint Ph.D. program grant (201506600024). This work was financially supported by the National Key Technology Research and Development Program of China (No. 2011BAD37B01), the Program for Changjiang Scholars and Innovative Research Team in University (IRT_15R09) and the Fundamental Research Funds for the Central Universities (2572014AA11). The Maoershan Forest Ecosystem Research Station provided field logistic support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.06.308>.

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